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EFFECTS OF COMMON ORIGIN AND COMMON ENVIRONMENT ON NESTLING PLUMAGE COLORATION IN THE GREAT TIT (*PARUS MAJOR*)

PATRICK S. FITZE,[1,2,3] MATHIAS KÖLLIKER,[2] AND HEINZ RICHNER[2,4]
[1]*University Pierre and Marie Curie-Centre National de la Recherche Scientifique, Laboratoire d'Ecologie, 7, quai Saint Bernard, Case 237, F-75252 Paris Cedex 05, France*
[2]*Institute of Zoology, Evolutionary Ecology Division, University of Bern, Baltzerstr. 6, CH-3012 Bern, Switzerland*
[3]*E-mail: patrick.fitze@esh.unibe.ch*
[4]*E-mail: richner@esh.unibe.ch*

Abstract.—Carotenoids cannot be synthesized by birds and thus have to be ingested with food, suggesting that carotenoid-based plumage coloration is environmentally determined. However signaling functions ascribed to plumage imply that plumage coloration is the outcome of an evolutionary process based on genetic variation. By means of a cross-fostering design we show significant effects of both a common rearing environment and the brood from which a nestling originally came from (common origin) on the plumage coloration of nestling great tits (*Parus major*). This demonstration of origin-related variation in carotenoid-based plumage coloration suggests that the observed variation of the trait has a partial genetic basis. Consistent with environmental determination of this trait, we also found a significant positive correlation between the color saturation of nestlings and their foster-father's plumage. There was no significant correlation between nestling plumage coloration and the food quantity provided to the nestlings by the male, the female, or both parents. This suggests that the nestling-foster father correlation arises by the carotenoid quantity ingested rather than the food quantity per se. No significant nestling-true father correlation was found, which suggests that nestling plumage coloration did not indirectly evolve due to sexual selection. Consistent with this result there was no significant correlation between the nestling's plumage color and its coloration as a breeding adult the following year, suggesting that nestling plumage color is a different trait than the first year plumage.

Key words.—Carotenoids, cross-fostering, food provisioning behavior, great tit, nestling plumage coloration, *Parus major*, signaling.

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In birds, carotenoid-based plumage coloration is common and has been suggested to serve various functions. Females may use carotenoid-based variation in plumage coloration during mate choice as an indicator of male quality, as demonstrated in the house finch *Carpodacus mexicanus* (Hill 1990, 1991), suggesting that the trait is sexually selected. Protection from predation by background matching of the plumage to the habitat (Brush 1978; Slagsvold and Lifjeld 1985), or signaling of condition toward predators (Fitzgibbon and Fanshaw 1988) suggests that carotenoid-based plumage colors can also arise by natural selection. However, many of the possible functions of plumage color have been investigated in adult birds only, and the evolution of nestling plumage color has been largely ignored. Plumage color of nestlings is most likely based on different selection pressures than adult coloration, and noncryptic colors may have evolved as a means of communication, and as a consequence of a parent-offspring conflict over resource distribution among young. For example, Lyon et al. (1994) have demonstrated that parents use the plumage coloration of individual young to adjust resource distribution among the offspring, suggesting that plumage color is used in parent-offspring communication.

Carotenoid-dependent yellow plumage coloration of nestlings, as observed in the great tit *Parus major*, is rare (Brush 1978, 1990), and the function and genetic basis of this trait is unknown. Here we investigate the heritable basis of variation in carotenoid-based nestling plumage color.

In the great tit, the yellow feather coloration of the nestlings is due to the carotenoids lutein and zeaxanthin. Both carotenoids are ingested with food (Partalli et al. 1987; Stradi 1998) and deposited without modification (as lipid-containing granules) in the follicular cells of developing feathers (Brush 1978). Thus, the feeding behavior of the parents and the availability of carotenoids in their territory may explain a considerable proportion of the color variation of nestlings among broods (Hõrak et al. 2000, Senar et al. 2002).

However, the proposed functions of plumage coloration are outcomes of evolutionary processes, and thus imply the presence of genetic variance for plumage color. The partitioning of the phenotypic variance into genotypic and environmental components is useful to estimate the degree to which a trait is genetically and environmentally determined (e.g., Boag and van Noordwijk 1987; Falconer and Mackay 1996; Lynch and Walsh 1998). In a cross-fostering experiment on great tits, we investigated origin-related (variance explained by the brood from which the nestlings originally came from) and environmental components of variance of the yellow nestling plumage coloration, and the resemblance between nestlings and their foster and true parents, respectively. In a regression of the nestling plumage coloration on the nestling's first year plumage coloration, we assessed whether nestling plumage predicts breeding plumage, as would be expected if nestling color evolved via correlated selection on adult plumage color.

MATERIALS AND METHODS

Experimental Procedures

To assess the degree to which plumage coloration of great tit nestlings can be accounted for by the brood from which a nestling originated (common origin) and a common environment we used a cross-foster experiment (Lynch and Walsh 1998). The experiment was performed in 1998 in a large

deciduous forest (the ''Forst'') near Bern, Switzerland. Hen fleas, common ectoparasites in great tit nests, are known to impair nestling growth and condition (Richner et al. 1993). Therefore all nests were heat treated within a microwave oven (Heeb et al. 1996) before egg laying to remove ectoparasites from the nest. By this procedure we avoided confounding variation leading to lower origin-related and higher environment-related estimates. Two days after clutch completion we measured egg mass. One day after the first nestling hatched, three nests with hatchlings of the same hatching date and with a similar number of hatchlings were assigned to a nest triplet. A total of 11 nest triplets (33 nests with a total of 289 hatched nestlings) were established. Within a nest triplet the broods were ordered according to mean body mass, whereas individual nestlings were ranked according to body mass within their brood of origin. Nestlings from the same origin were then distributed over the two other broods of the same nest triplet according to their rank within their brood of origin and the rank between the potential foster broods, following the procedure described by Brinkhof et al. (1999) and Koelliker et al. (2000) for experiments using similar designs. The nestling ranked first in its nest of origin was assigned to the heavier foreign brood, the nestling ranked second to the lighter foreign brood, then the nestling ranked third was again assigned to the heavier foreign brood, and so on until all nestlings of a given origin were distributed over the two foreign nests. The nestlings of the two other broods of a nest triplet were exchanged following the same procedure. To avoid manipulation of brood size, no further nestlings were added to a nest when its original nestling number (i.e., the number before cross-fostering) was reached. Therefore, 51 nestlings (of 27 different origins) of a total of 289 hatched nestlings were not cross-fostered and thus remained in their home nest. These nestlings were excluded from further analysis to ensure that only nestlings fed by unrelated parents were analyzed. By this design the within-brood variances in body mass (after cross-fostering) were kept close to the initial variances, although nestlings of the same origin were adequately distributed with respect to their individual rank within the newly created foster broods. Hatchlings were marked individually by clipping one or two of the six down feather tracts, and by ringing them with numbered aluminium rings nine days after hatching.

Feeding Behavior

Feeding rates were recorded nine days after hatching with an infrared-sensitive video camera as described in Christe et al. (1996). Nest triplets were filmed simultaneously ($\pm$ 1 h). For the analysis of the videotapes, the first 30 min of the film were discarded to exclude observations influenced by disturbance to the nest when setting up the camera. Food provisioning rates (number of nest visits with food provisioning) of the male and female parent were measured during the subsequent 30 min.

Adult measurements

Fourteen days after the first nestling hatched, parents were caught at the nest. For both nestlings and parents, we measured tarsus length with a calliper to the nearest 0.1 mm, body mass with a Sartorius electronic scale (SartoriusAG, Goettingen, Germany) to the nearest 0.1 g, and we took a digital picture of the breast plumage measuring the red-green-blue (RGB) color values. In the following year (1999) we recaptured the cross-fostered nestlings, now breeding in our study area, 14 days after hatching of their offspring and took a digital picture of their breast plumage.

Color Quantification

To take a picture we first smoothed the plumage and then placed the bird in a box, upholstered with foam material to prevent it from moving. The box was covered by a photographic filter (Hoya UV-filter, 59 $\times$ 74 mm, Hoya Corp., Tokyo) and a thin cardboard strip at one end to protect the bird's eyes from the flash. Standard white chips (Kodak Color Control Patches with red = 255, green = 255, blue = 255) were fixed to each side of the filter for calibration of the equipment during color analysis. The box was placed in a standard position inside a larger camera box. Two flashes (factory-calibrated Nikon SB26) were mounted at an angle of 13° to the optical axis, 10 cm below and 20 cm beside the front lense of the camera (Nikon E2 with a 105mm f/2.8 Nikkor lense). The distance between the feathers and the front lens was fixed to 50 cm. The settings of the camera and flashes were kept constant, and thus all pictures received a standardized light exposure. The pictures were imported into the Adobe Photoshop program, and a virtual second layer, holding ten squares of 400 pixels each, was placed over the picture in a standard position with respect to the box. The program then calculated the mean RGB values for each square. The squares with visible down feathers, and in adults the squares falling on the black breast stripe, were excluded from the analysis. There was no correlation between the color values and the number of squares analyzed (R: $r = -0.01$, $P = 0.90$; G: $r = 0.02$, $P = 0.81$; B: $r = 0.04$, $P = 0.62$; $n = 191$ birds), indicating that the exclusion of squares did not bias the results. Both the photograph and the analyses were done blindly with respect to origin and condition of the birds.

Mean RGB-values per bird were converted to hue-saturation-brightness (HSB-) values by the algorithm described in Foley and Van Dam (1984). The variation in light exposure, as assessed from the measurements of the white reference chips, was small (R: 253 $\pm$ 0.08 SE, G: 252 $\pm$ 0.09 SE, B = 240 $\pm$ 0.11 SE), and therefore no correction of the color values measured on the plumage was required. To assess repeatability of color assessment with this method, seventeen nestlings were placed twice in the photographic box and a digital picture taken. Repeatability of color parameters (Lessells and Boag 1987), was significant (H: r (repeatability) = 0.60, $F_{1,10} = 9.87$, $P < 0.001$; S: $r = 0.72$, $F_{1,10} = 16.13$, $P < 0.001$; B: $r = 0.49$, $F_{1,10} = 6.83$, $P < 0.001$).

The measures of color used here likely do not correspond exactly to the colors perceived by the birds. Also birds possess receptors for Ultra violet light (e.g., Bennett et al. 1996, 1997; Andersson and Amundsen 1997; Andersson et al. 1998; Johnsen et al. 1998; Cuthill et al. 1999; Hunt et al. 1998; Keyser and Hill 1999), which was not detected by our equipment. However, as Bennett et al. (1994) remarked ''for heuristic purposes, it may be useful to express color patterns in

subjective terms that humans can readily understand'' especially if these are repeatable, standardized, and blind with respect to treatment, as in this study.

It is well documented that the yellow plumage coloration of the great tit is the product of carotenoid incorporation into the feathers (e.g., Goodwin 1980; Partalli et al. 1987; Britton et al. 1995; Stradi 1998). To understand the relationship between carotenoid availability, carotenoid content of the feathers, and plumage coloration we performed an experiment for another purpose, where half of the nestlings of a brood was supplied with additional carotenoids while the other half was fed a placebo (Tschirren et al. 2003). We found highly significant differences in the plumage coloration between supplemented and placebo-fed nestlings ($F_{1,48} = 106.34$, $P < 0.0001$). Thus, our method of color quantification provides a correlate of the amount of carotenoids incorporated into the feathers.

Statistical Analyses

Thirty-two of 238 exchanged nestlings (from 18 different origins) died before we could take a picture of their plumage. Fifteen nestlings which showed a poorly developed plumage were excluded from the analysis because we could not measure the yellow in at least one of the 10 square measurement areas. Thus, the analysis was performed on the remaining 191 nestlings (of 33 different origins). Not all parents could be caught and therefore sample sizes for parent-offspring correlations were less than 33 (31 in females, 28 in males, and 27 for midparents). Due to occasional technical problems with video cameras, not all nests could be filmed and this reduced the sample size for the feeding rates to 24 nests.

Hue, saturation, brightness, and the overall plumage coloration were analyzed using nested Anova with random effects (Model II) with both nest of growth and nest of origin nested within triplets. The nest of origin accounts for variation before cross-fostering. It therefore includes genetic effects, maternal effects, and effects due to the common environment before cross-fostering. The nest of growth accounts for the variation that arises after cross-fostering. It therefore includes effects related to the foster parents, for example, territory quality, feeding behavior, and effects of the foster nest. Nested analysis within experimental triplets corrects for seasonal effects because nestlings within triplets hatched the same day. We defined nestling condition as the residuals of the regression of nestling body mass on nestling tarsus and included it as a covariate in the model. To evaluate the overall plumage coloration, we used the first principal component (PC1) from a principal component analysis including hue, saturation, and brightness; PC1 explained 61.3% of the total variance of the combined color variables in nestling great tits (factor loadings: H: −0.59; S: 0.67; and B: 0.45).

Females breeding early in the season had a more saturated plumage than females breeding later ($n = 30$, $r = -0.494$, $P = 0.006$, $P < 0.05$ after correction for multiple comparisons). This indicates that parents within nest triplets have more similar plumage coloration than expected by chance due to seasonal effects arising from environmental and/or genetic variation. We accounted for these effects by including a factor for nest triplet in the models, leading to a conservative estimate of the origin-related variance.

We performed parent–midoffspring regressions to assess whether nestling plumage coloration is related to parental coloration and more specifically to assess whether it is related to origin (true parent) and/or environment (foster parent) (Falconer and Mackay 1996; Lynch and Walsh 1998). Heritability estimates were calculated from parent-offspring regressions by doubling the single-parent midoffspring regression coefficients (Table 2), following Lynch and Walsh (1998). The parental color values (H, S, B, and PC1, respectively) were standardized for the nest triplet by using the residuals of a one-way ANOVA with nest triplet as a factor. In parent–midnestling correlations, nestling color values were standardized for the rearing environment by calculating the residuals of a model II nested ANOVA with nest triplet as an independent factor and the nest in which young were reared (nest of growth) nested within nest triplet. For the foster parent–foster nestling analysis, nestling color values were standardized for the nest of origin using the residuals of a model II nested ANOVA with nest triplet as an independent factor and the nest of origin nested within nest triplet.

To analyze maternal effects arising through egg mass, we estimated the correlation between egg mass and nestling plumage color. However, we could not determine if other maternal effects arising through different egg contents (e.g., differences in carotenoid content) were present. The color values that were used in the correlation were standardized for the rearing environment, as in parent–midoffspring correlations. Percentages of feeding rates (e.g., male feedings per total feedings) were square-root arcus sinus transformed before analysis (Sokal and Rohlf 1981). All feeding variables were standardized for the nest triplet. Normality of the data was evaluated by the Lilliefors' test (Wilkinson 1989). All tests are two-tailed and the significance level is set at $P = 0.05$. Sequential Bonferroni corrections were used to adjust the *P*-values for the increased probability of achieving statistical significance from multiple tests (Rice 1989). Statistical analyses were performed with the JMP statistical package (Sall and Lehman 1996).

RESULTS

Sibling Comparison

Common origin had a significant effect on color saturation and overall plumage coloration (PC1) of nestlings, but no significant effect on hue and brightness (see Table 1). The variance component due to common origin explained 14.66% of the total variance in plumage saturation and 11.73% of overall plumage coloration (PC1). The common rearing environment significantly affected hue, saturation, and the overall plumage coloration (PC1), but not brightness (see Table 1). The variance components due to common rearing environment explain 30.87% in hue, 36.62% in saturation, and 26.84% in the overall plumage coloration of the total variance of each color variable.

Parent-Offspring Comparison

None of the four response variables of the nestling plumage coloration correlated significantly with the values of their

TABLE 1. Analysis of the effects of common origin and common environment on plumage color of nestling great tits.

	Factor	Sum of squares	df	*F*	*P*	Variance explained
Hue	nest of growth [nest triplet]	38.85	19, 139	3.25	<0.0001**	30.87%
	nest of origin [nest triplet]	22.44	22, 139	1.62	0.049	8.79%
	nest triplet	22.30	10, 18.9	0.73	0.692	0%
Saturation	nest of growth [nest triplet]	0.072	19, 139	4.31	<0.0001**	36.62%
	nest of origin [nest triplet]	0.044	22, 139	2.28	0.002**	14.66%
	nest triplet	0.062	10, 22.9	0.98	0.488	0%
Brightness	nest of growth [nest triplet]	0.035	19, 139	1.23	0.319	3.79%
	nest of origin [nest triplet]	0.037	22, 139	1.13	0.319	2.32%
	nest triplet	0.090	10, 8.3	4.07	0.027	20.39%
Overall coloration[1]	nest of growth [nest triplet]	63.99	19, 139	3.09	<0.0001**	26.84%
	nest of origin [nest triplet]	45.21	22, 139	1.89	0.015*	11.73%
	nest triplet	69.98	10, 20.3	1.28	0.302	4.90%

* $P < 0.05$ after Bonferroni adjustment; ** $P < 0.01$ after Bonferroni adjustment.
[1] Overall plumage coloration (PC1) combines hue, saturation, and brightness.

true parents (see Table 2). However, there was a significant and positive regression between nestling plumage saturation and their foster father's saturation (see Fig. 1A). The foster mother-nestling regression for saturation was not significant (see Fig. 1B) and similarly the midparent-nestling regression was not significant. Neither brightness and hue, nor the overall plumage coloration of the nestling plumage, were significantly correlated with the corresponding foster mother's or foster father's color parameters. No assortative mating based on plumage color could be detected (nonstandardized male vs. female plumage variables: H: $n = 27$, $r = 0.24$, $P = 0.23$; S: $n = 27$, $r = 0.33$, $P = 0.09$; B: $n = 27$, $r = 0.29$, $P = 0.14$; PC1: $n = 27$, $r = -0.03$, $P = 0.87$). This suggests that the correlation between foster father and nestling saturation was not indirectly mediated by the plumage saturation of the female.

Nestling Plumage—Adult Plumage Correlation

Twenty of the 191 experimental nestlings (ten females and ten males) were recaptured the following year as breeding adults. The plumage coloration of these nestlings was not significantly correlated with their first-year plumage coloration (before Bonferroni correction: males, $n = 10$; H: $r = -0.27$, $P = 0.45$; S: $r = 0.58$, $P = 0.08$; B: $r = 0.33$, $P = 0.36$; females $n = 10$; H: $r = 0.16$, $P = 0.66$; S: $r = -0.01$, $P = 0.98$; B: $r = 0.24$, $P = 0.50$).

Correlates of Plumage Coloration

Egg mass

Color parameters of nestlings were not significantly correlated with egg mass, as shown by an analysis among nests of mean egg mass within a clutch against mean residual color of nestlings hatched from these eggs (hue: $r = -0.105$, $P = 0.56$; saturation: $r = 0.04$, $P = 0.81$; brightness: $r = 0.02$, $P = 0.92$; PC1: $r = 0.07$, $P = 0.69$; $n = 33$).

Nestling body condition

Nestling condition, when included as a covariate in the nested-ANOVA model (see Table 1), showed a significantly positive relationship with brightness, but not with hue, saturation and PC1 (B: $F_{1,138} = 7.37$, $P = 0.008$ [$P < 0.05$ after Bonferroni correction] H: $F_{1,138} = 2.74$, $P = 0.10$; S: $F_{1,138} = 0.83$, $P = 0.37$; PC1: $F_{1,138} = 0.46$, $P = 0.50$). Inclusion of condition had no effect on the significance levels shown in Table 1, suggesting that the variation explained by the factors of the model is independent from the effects of body condition on plumage coloration.

Food provisioning behavior

Experimental work strongly suggests that variation in males' coloration arises by carotenoid limitation in its habitat (Hill

TABLE 2. Parent–midnestling regressions.

	Midparents			Females			Males		
	h^2† ± SE	*n*	*P*	h^2 ± SE	*n*	*P*	h^2 ± SE	*n*	*P*
True parents									
Hue	0.168 ± 0.141	27	0.25	0.268 ± 0.181	31	0.15	0.048 ± 0.199	28	0.82
Saturation	0.080 ± 0.140	27	0.57	0.085 ± 0.178	31	0.64	0.187 ± 0.256	28	0.47
Brightness	−0.048 ± 0.127	27	0.71	−0.145 ± 0.162	31	0.38	0.067 ± 0.210	28	0.75
PC1	−0.133 ± 0.144	27	0.36	−0.045 ± 0.167	31	0.78	−0.171 ± 0.194	28	0.39
Foster parents									
Hue	0.078 ± 0.163	27	0.63	0.128 ± 0.220	30	0.57	0.096 ± 0.227	27	0.68
Saturation	0.341 ± 0.154	27	0.04	0.116 ± 0.216	30	0.59	0.848 ± 0.261	27	0.003*
Brightness	−0.009 ± 0.119	27	0.94	−0.078 ± 0.157	30	0.62	0.032 ± 0.198	27	0.87
PC1	0.201 ± 0.152	27	0.20	0.256 ± 0.183	30	0.17	−0.003 ± 0.218	27	0.99

* $P < 0.05$ after Bonferroni adjustment.
† Heritability estimates (h^2) are shown (see statistics).

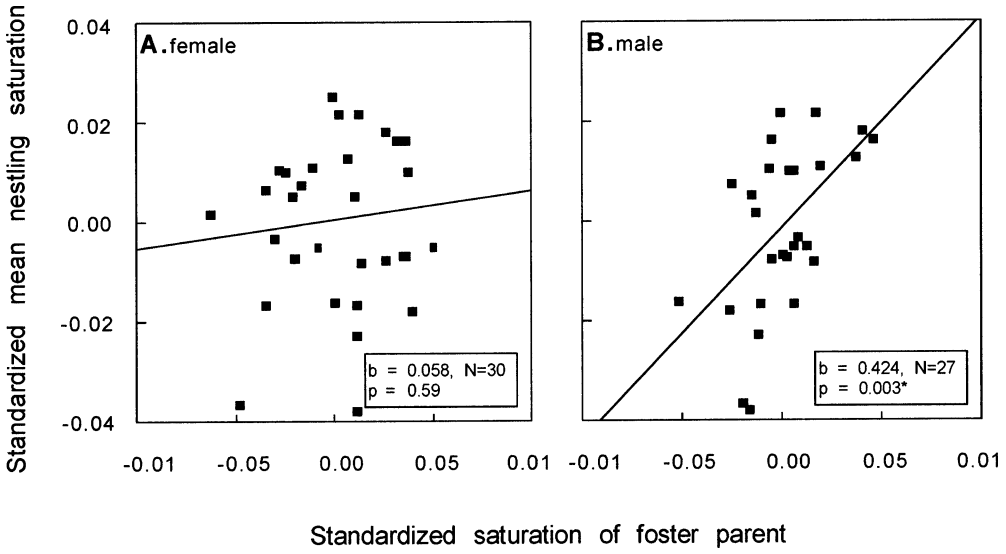

FIG. 1. Foster parent-midfoster nestling regression of plumage saturation. A. Female–midfoster nestling regression. B. Male–midfoster nestling regression (for standardization see methods), including the slope (b) of the least-square regression, *P*-values, and number of nests.

1992). As we found a significant and positive foster father–midoffspring regression we expect a positive correlation between the plumage saturation of the foster nestlings and the territory quality of the foster males, and thus the quantity or quality of food provisioned by the foster parents. However, the mean plumage saturation of foster nestlings was not related to the overall rate of food provisioning by the foster parents (ANCOVA: $n = 24$, $F_{1,23} = 0.258$, $P = 0.62$).

DISCUSSION

Effects of the common origin

Our study shows a significant effect of both a common origin and a common rearing environment on nestling plumage saturation. The significant contribution of the common origin in saturation suggests a genetic basis of the nestling plumage coloration. This genetic basis may arise by genetic determination of at least three different physiological mechanisms involved in color expression: the carotenoid absorption through the intestinal mucosa, the carotenoid transportation in the blood, and/or the carotenoid deposition in the follicular cells of the feathers (Brush 1990, McGraw and Hill 2001, McGraw et al. 2002). Two additional nonexclusive hypotheses, such as maternal effects before hatching or effects of the common environment before cross-fostering, may contribute to the observed effect of the common origin. Because the eggs of great tits contain considerable amounts of carotenoids (Partalli et al. 1987; Blount et al. 2000), a maternal effect could arise through variation in carotenoid quantity transferred to the egg yolk. Females could either lay eggs of different mass or eggs of different carotenoid content per egg volume. In this study, origin-related effects due to different egg mass can be excluded, because we did not find a significant correlation between egg mass and nestling coloration, but differences in carotenoid content cannot be excluded.

The plumage coloration of nestlings and adults may be two genetically uncorrelated traits that evolved independently. Under this assumption parental plumage coloration would not predict offspring plumage coloration and thus no true-midparent-offspring, no true-father-offspring, and no true-mother-offspring regressions should exist. This hypothesis would be further supported by a lack of a significant correlation between the nestling and the first year plumage coloration (the breeding plumage coloration). Our data confirms this hypothesis because we did not find either a significant true-parent, true-father, or true-mother-offspring regression, or a significant correlation between nestling and first year plumage. These two lines of evidence suggest that the nestling plumage coloration did not indirectly evolve as a correlated trait due to sexual selection on carotenoid-based adult plumage coloration (Hõrak et al. 2001). For the comparison of nestling and adult plumage, sample sizes were low, and therefore power for testing the hypothesis that nestling and adult plumage are independent traits. However, two other hypotheses may predict the same results. First, parents may have developed their breeding plumage under different environmental conditions than their offspring, which may largely override origin-related effects (Roff 1997). Second, the lack of a significant parent-offspring regression might be due to a lack of statistical power. While in the nested ANOVA, 191 nestlings were analyzed, thus the parent-offspring correlation was based on the 31 corresponding pairs of adult birds. The applied design does not allow discriminating between these three hypotheses.

Environmental Effects

Hill (1992) previously showed that plumage coloration is affected by environmental factors. Experimental manipulation of environmental conditions, such as food availability (Hill 1992, 2000) and state of health (Hill and Brawner 1998), caused changes in plumage coloration in house finches. Consistent with these findings, the comparison of cross-fostered

siblings in the present study shows that hue, saturation, and the overall coloration of the nestling plumage are significantly influenced by the common rearing environment (see Hõrak et al. 2000; Senar et al. 2002). Also, the significant positive regression between plumage saturation of foster fathers and of nestlings indicates that nestling plumage saturation is influenced by the environment.

Several studies suggest that the carotenoid-dependent coloration is a condition-dependent trait (Hill 1990; Hill and Montgomerie 1994; Hill and Brawner 1998; von Schantz et al. 1998; Grether et al. 1999; Keyser and Hill 1999; Hõrak et al. 2000; but see McGraw and Hill 2001). These suggestions are supported by our data since nestling body condition at fourteen days posthatching is significantly correlated with variation in plumage coloration despite the effects of a common environment. This shows that, besides nestling condition, other environmentally determined factors not investigated in this experiment, may play an important role for plumage coloration.

Many studies have shown that territory quality strongly affects reproductive performance, as measured by the number and mass of eggs and number of nestlings and fledglings (Seki and Takano 1998). Furthermore, coloration has been shown to correlate with food availability in the territory (Slagsvold and Lifjeld 1985; Eeva et al. 1998). Nestlings raised by parents of good territories may therefore obtain more food, or food containing more carotenoids, resulting in more saturated nestling plumage compared to nestlings raised in poor territories (Slagsvold and Lifjeld 1985, Hõrak et al. 2000). Because adult great tits are very territorial throughout the year, including the period of molt (e.g., Drent 1983), the plumage of both nestlings and parents would be similarly affected by territory quality. Nestlings growing up in a carotenoid rich territory should develop a more saturated plumage. Thus, a positive correlation between the foster father's and the nestling's plumage coloration would be predicted. This prediction is not directly supported by our data, as the summed feeding rate of male and female parents (i.e., territory quality in terms of prey availability), was not correlated with mean nestling plumage saturation. Therefore, territory quality does not seem to affect nestling saturation through prey quantity, but might be a function of the carotenoid-content of the prey.

The positive foster father-nestling plumage coloration may arise by at least two other mechanisms. First, the males' food provisioning rates may correlate with their plumage coloration, as observed in northern cardinals *Cardinalis cardinalis* (Linville et al. 1998), where bright males provided the nestlings with more food than the pale males. Alternatively, the more colored males might provision young with more carotenoid-rich food. Both hypotheses predict a positive correlation between nestling and foster father plumage coloration, but no correlation between the foster female and nestling plumage coloration. No significantly positive correlation between male plumage saturation and male feeding rate (feeding rate: $n = 21$, $F_{1,20} = 3.01$, $P = 0.10$) was observed in our study. Thus, our results are not explained by variation in food quantity. Second, if female investment depends on male quality, (Burley 1988) with females mated to males with more saturated plumage providing nestlings with more food or food of higher carotenoid content, we would also observe a positive foster father-offspring correlation. However female food provisioning rate was not significantly correlated with male plumage saturation ($n = 21$, $F_{1,19} = 1.44$, $P = 0.25$) and the proportion of total feedings provided by the foster male was negatively correlated with nestling plumage coloration (proportional feeding rate: $n = 24$, $F_{1,23} = 6.775$, $P = 0.016$, $P < 0.05$ after Bonferroni correction; see Fig. 2). Although the carotenoids incorporated into the nestling's feathers have to be ingested with the food, our results do not directly support one of the above hypotheses suggesting that the carotenoid quantity rather than the quantity of food ingested should be analyzed.

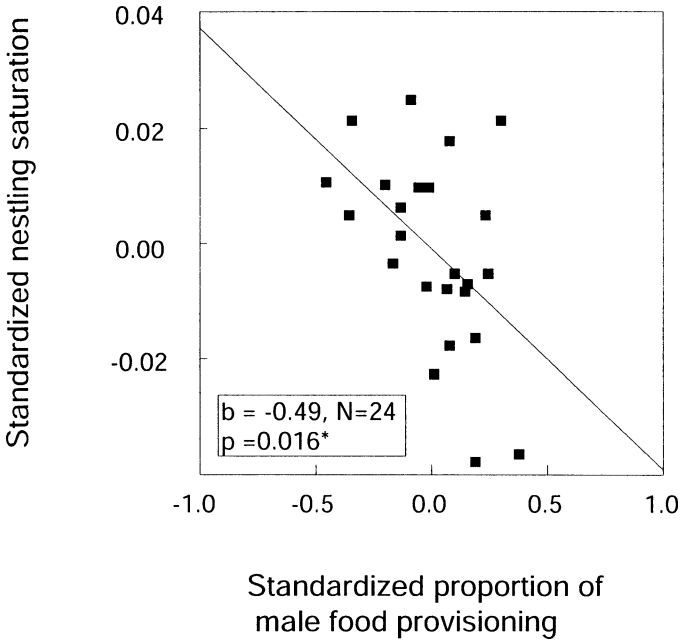

FIG. 2. Regression between the proportion of total feedings provided by the foster male and nestling plumage saturation (for standardization see methods), including the slope (b) of the least-square regression, *P*- values, and number of nests.

In conclusion, our study suggests that nestling plumage coloration is not purely environmentally determined, as could be expected due to the mechanism of direct carotenoid incorporation into feathers, but also seems to have a genetic basis. Thus, nestling plumage coloration may respond to selection arising through one or several of the proposed signaling functions (i.e., background-matching, signaling toward predators, signaling toward parents). Nestling and adult plumage coloration may have a different genetic basis, and thus nestling plumage coloration will have evolved due to selective pressures unrelated to sexual selection.

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